mechanical work, but the cycle was incomplete. When erosion supervened and conferred upon the superficies of the continents a certain mobility and kinetic energy, the cycle was completed and the stage answering the adiabatic expansion was supplied.

It is true that the efficiency of this engine must be very small, but the store of energy upon which it draws—the available boiler capacity—is enormous. The mechanism thus appears competent to bring about all of the dynamical effects with which geology has to deal.

[1] H. Nagaoka, *Phil. Mag.*, **50**, 53 (1900).
[2] Simultaneous joints. *Proc. Wash. Acad.* **7**, 267 (1905).
[3] Becker, *J. Wash. Acad.*, **4**, 429 (1914).
[4] Ibbetson, *Math. Theory of perfectly elastic solids*, 1887, p. 174.

A PHYLOGENETIC STUDY OF CYCADS

By Charles J. Chamberlain
DEPARTMENT OF BOTANY, UNIVERSITY OF CHICAGO
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In any phylogenetic study it is desirable to compare related forms which are widely separated in time and space. In case of the cycads, such comparisons are becoming possible. The general plan of an investigation, begun more than ten years ago, is to study numerous forms in the field; study life histories in all parts of the family; and then, by comparative study, to gain some idea in regard to relationships and also in regard to the behavior of various structures during great periods of time.

A typical cycad, with its unbranched trunk and crown of pinnate leaves, looks like a tree fern, an aspect which dates back as far as anything is known about the phylum.

In the Carboniferous, two great lines of seed plants were abundant and widely distributed. One of them is represented today by such familiar forms as the pines, junipers, araucarias and taxads. They are mostly evergreen, are widely distributed, and form immense forests. Being easily available, they have been thoroughly studied, especially the north-hemisphere genera. The other line is represented by a single living family, the Cycadaceae, or cycads, as they are commonly called. The Paleozoic ancestors of the cycads had a world-wide distribution and made such a display that botanists have called the Paleozoic the Age of Ferns, since the leaves were very naturally mistaken for fern leaves. These fern-like seed plants undoubtedly came from an even earlier fern ancestry and, in the Carboniferous, existed side by side with

true ferns; but, whether a given specimen should be assigned to the ferns or to these primitive seed plants, cannot be determined by the leaves alone. The only decisive character is the seed.

From splendidly preserved material, English botanists have been making a vigorous study of this group, so that their results are available for comparison. Their researches have covered the external form and also the internal structure of the stem, leaf, root, microsporangium and megasporangium; but, as yet, almost nothing is known about the gametophytes and embryo.

A Mesozoic order—known as the Bennettitales—which may have been the predecessor of the cycads, was also fern-like in appearance. These forms still retained the unbranched trunk and crown of pinnate leaves, so characteristic of ferns and Paleozoic seed plants; but only pinnae of the simplest type persisted and the trunk was short and stocky, so that in general appearance they bore more resemblance to the modern cycads than to their Paleozoic ancestors. The microsporangia were borne on a whorl of leaves, reduced considerably, but still retaining the pinnate character of the foliage leaves. The seed bearing structures, however, were collected into a compact cone, in which no one but a morphologist would recognize the homologues of leaves. Both the pollen producing and the ovule bearing leaves were in the same strobilus, so that the bisporangiate strobilus is a striking feature of the group, or at least, of its upper Mesozoic members. These strobili were small and numerous and were borne in the axils of foliage leaves. The material which has been under investigation has come from Idaho, Dakota, Maryland, Mexico, Europe and India; but this does not mean that the group was confined to the northern hemisphere, for these places are all in the university belt or are easily reached from universities. Forms which may belong here, or may belong to the true cycads, occur in Cretaceous deposits in South Africa, and vast regions remain to be explored.

G. R. Wieland has made the most extensive contributions in this field, but, as in case of the Paleozoic members of the phylum, scarcely anything is known of the gametophytes and not much is known about even the sporophyte structures of Triassic forms.

While I have studied, with great interest, the best material of the Paleozoic and Mesozoic forms, my own research has been confined to the only living family of the phylum, the Cycadaceae, or cycads.

The geological history of the cycads is still very indefinite, largely because stem and leaf characters are hardly sufficient to distinguish true cycads from the Mesozoic Bennettitales. The confident determina-

tions which one sees in museums bring to mind the so-called ferns of the Paleozoic. However, some of the living genera are distinguishable in the Tertiary and it is possible that the family goes back even to the Triassic. The resemblance of the stems and leaves of the living cycads to those of the Bennettitales is too striking to be accidental; on the other hand, there is nothing in the seed-bearing cones of any of the Bennettitales yet described which could have given rise to the seed-bearing cones of the living cycads. Further investigation, especially of Triassic forms, must be made before one can say with any confidence whether the modern cycads have come from the Bennettitales, or both have come from the Paleozoic Cycadofilicales.

The geographic distribution of the living cycads is very restricted. All are tropical or subtropical. Four of the nine genera belong to the western hemisphere and five to the eastern, there being no genus common to both hemispheres. With two exceptions, the genera are very local in their distribution. In the western hemisphere, the thirty-odd species of *Zamia* range from Florida to Chili; while, in the eastern hemisphere, the dozen species of *Cycas* range from Japan to Australia. Two genera are found only in Mexico; one only in Cuba; two only in Australia, one of these being confined to Queensland; and the other two are found only in South Africa. So, with the exception of the two genera which cross the equator, the western genera are in the northern hemisphere and the eastern genera are in the southern. Even in the places mentioned, the plants occur singly or in scattered groups. There is no such things as a cycad forest.

Perhaps, later, it may be possible to give some reason for this peculiar distribution and for the scarcity of individuals.

The nine genera of living cycads are so sharply defined that there is no difficulty in recognizing them. In herbarium specimens, this rigidity extends to species, and, before I began to study cycads in the field, I supposed that the species were rather sharply marked. By the time I had made four excursions into the Mexican tropics, it was evident that species could vary, even in *Dioon* and *Ceratozamia*. However, I was not prepared for the bewildering maze of forms which I found as I tramped the *Macrozamia* regions of Australia. Three species, with erect cylindrical trunks, are easily distinguishable, but I was almost tempted to say, "Call the rest *Macrozamia spiralis*, and let them go." Taxonomists describe several species of the South African genus, *Stangeria*, but, after wandering over nearly the entire range of the genus, from Zululand to Port Elizabeth, I should not be surprised if all of them should be raised from the seeds of a single cone. Some species of the African

genus, *Encephalartos*, seem comfortably distinct, while others are so variable that one could identify herbarium specimens with more assurance than he could plants in the field.

An experimental study of variation in cycads is not attractive. *Dioon edule* probably reaches an age of fifty years before it produces cones; *Macrozamia Moorei* has been known to cone at twenty years; some species of *Zamia* may cone at ten years, or even less; but the succession of generations is too slow for any experimental work involving the whole life history. Seedlings of all the genera and many of the species are growing at the University of Chicago and it is evident that there is considerable variation in the seedlings from a single cone. Some work in hybridization is being attempted and one might reasonably hope to see results if any should appear in the first generation.

In comparing Paleozoic, Mesozoic and living members of the phylum, it is evident that the Mesozoic forms are larger than the Paleozoic, and that the living forms are still larger than the Mesozoic. Some of the seeds of the Paleozoic forms were very small, but some were larger than any yet known in the Mesozoic, yet none even approached the large seeds of some of the living cycads. Cones of the Bennettitales can be carried in the pocket, but some of the cones of living cycads reach a weight of ninety pounds. While the sperms of the fossil forms have never been identified with certainty, the structure of the ovules makes it certain that they could not have been nearly so large as those of the living cycads. On the whole, there has been an increase in size as we pass from the Paleozoic to the living forms.

In all the living Gymnosperms, the development of the female gametophyte begins with a series of free nuclear divisions which is followed by cell formation. Undoubtedly, the lowest seed plants came from heterosporous Pteridophytes, and it is more than probable that these heterosporous Pteridophytes of the Paleozoic had female gemetophytes beginning with free nuclear division, although the earliest heterosporous forms, just emerging from the homosporous condition, probably had female gametophytes in which all nuclear division was accompanied by the formation of walls. No homosporous form, either living or fossil, shows free nuclear division at this stage in the life history. Free nuclear division came with the increase in the size of the spore, and the extent of the free nuclear period is more or less correllated with the size of the spore. In the large megaspores of *Dioon* there may be thousands of free nuclei before wall formation begins; in the smaller megaspores of *Zamia*, only hundreds.

That the theory, just expressed, is correct, is indicated by the early development of the sporophyte in Gymnosperms. The eggs are large, and—with two or three exceptions—fertilization is followed by a period of free nuclear division before walls begin to appear. In the two or three exceptions, the egg is small, and the first division of its nucleus is followed by the formation of a wall. In all Angiosperms, the egg is small and a wall follows the first division of its nucleus.

Thus we have a series beginning with the homosporous Pteridophytes in which a wall always followed the first division of the spore, free nuclear division appearing somewhere, as heterospory was attained and the megaspore increased in size; the free nuclear period becoming more prolonged in the larger megaspores of the Gymnosperms, then culminating and beginning to decline in the cycads. The series is even more striking in case of the embryo, since there is the same increase, culmination and decline of the free nuclear period and a few Gymnosperms, together with all Angiosperms have come back to the original condition in which a wall follows the first nuclear division of the egg.

Some of the microscopic details are remarkably constant, e.g., in the pollen tube of all the genera the prothallial cell presses deeply into the body cell. The cycads can be distinguished from all other living seed plants by this cytological character. In all the genera, two blepharoplasts appear in the body cell and, in the two sperms derived from it, develop into coiled bands bearing thousands of cilia by means of which the sperm becomes a vigorous swimmer. Since these details are so uniform, they must antedate the differentiation into the modern genera. On the other hand, there are characteristic differences in the pollen tubes and their contents, so that the pollen tube structures will not only distinguish the family from other seed plants, but will distinguish the genera from each other.

The foregoing paragraphs are intended to indicate the drift of a few phases of an investigation which has been in progress for more than ten years. So far, only scattered descriptive sketches have been published, but all the genera and many of the species have been studied in the field and material has been collected for detailed studies of practically all phases of the life histories. Besides, obliging correspondents in Cuba, Mexico, Australia and Africa are constantly sending field notes, photographs and material, so that, in time, the interrelationships of the genera and the origin of the family may be cleared up and some opinion may be ventured in regard to phylogenetic characters and their gradual modification.